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Structure and distribution of sensilla coeloconica on the maxillipedes of Chilopoda

by

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ABSTRACT

Scanning and transmission electron microscopic investigations of the maxillipedes of adult centipedes and the first anamorphic larval stage of Lithobiomorpha show the presence of sensilla coeloconica on the surface of the poison claw. In maxillipedes of larval stages only a single type of sensillum is present. In the adult centipedes three types of sensilla coeloconica were observed: (I) thick conical sensilla, (II) thin slender sensilla, and (III) long and tapered sensilla. The distribution of these types on the surface of the poison claw of the maxillipede is shown. Each sensillum coeloconicum consists of a short peg in a round or oval cuticular pit. A terminal pore on the tip of each peg suggests that all these sensilla coeloconica have a chemoreceptive function. Tubular bodies in the type II sensilla of *Lithobius forficatus* (Linnaeus, 1758) point to a mechanoreceptive function which means that the thin sensilla coeloconica may function as contact chemoreceptors. The two different types of dendritic outer segments in the type I sensilla of *Necrophloeophagus longicornis* (Leach, 1815) and *L. forficatus* point to a double function, perhaps to hygro- or thermoreception. The phylogenetic significance of the presence of three types of sensilla coeloconica in the five orders of centipedes is discussed.

INTRODUCTION

The maxillipedes (forcipules) of centipedes, with their powerful poison claws, play an important role in capturing and killing their prey. The cuticular sensilla on the surface of the claws was first demonstrated using a Scanning Electron Microscope (SEM) in *Scolopendra morsitans* by Jangi & Dass (1977) and later in *Ethmostigmus rubripes* (Brandt, 1848) by Menez *et al.* (1990). Each sensillum consists of a short cone situated in an oval pit. Jangi & Dass (1977) noticed that each conical receptor bears a depression distally, where its wall is apparently delicate and membranous and possibly pervious to chemical stimuli. Jangi & Dass (1977) and Menez *et al.* (1990) thought the sensilla were chemoreceptors, which was demonstrated by Jangi & Dass (1977) in stimulation experiments.

Further scanning electron microscope examinations demonstrate that cuticular sensilla coeloconica are present on the maxillipedes of the first anamorphic larval stages of Lithobiomorpha and in adult species of Scutigeromorpha, Lithobiomorpha, Craterostigmomorpha, Scolopendromorpha, and Geophilomorpha (Ernst 1995 1999 *a,b*; Ernst & Rosenberg 2001). The first ultrastructural studies concerning these structures were presented by Ernst (1995) for *Necrophloeophagus longicornis* and by Rosenberg & Ernst (2001) for *Lithobius forficatus*. The aim of this paper is to describe the arrangement of the different types of sensilla coeloconica on the poison claws of centipedes and to discuss the phylogenetic significance of these structures.

MATERIAL AND METHODS

The heads of anamorphic larval stages I and II of *L. mutabilis* (C. L. Koch, 1862) and *L. dentatus* (C. L. Koch 1844) and of adult *L. scutigera, Scutigera coleoptrata* (Linnaeus,

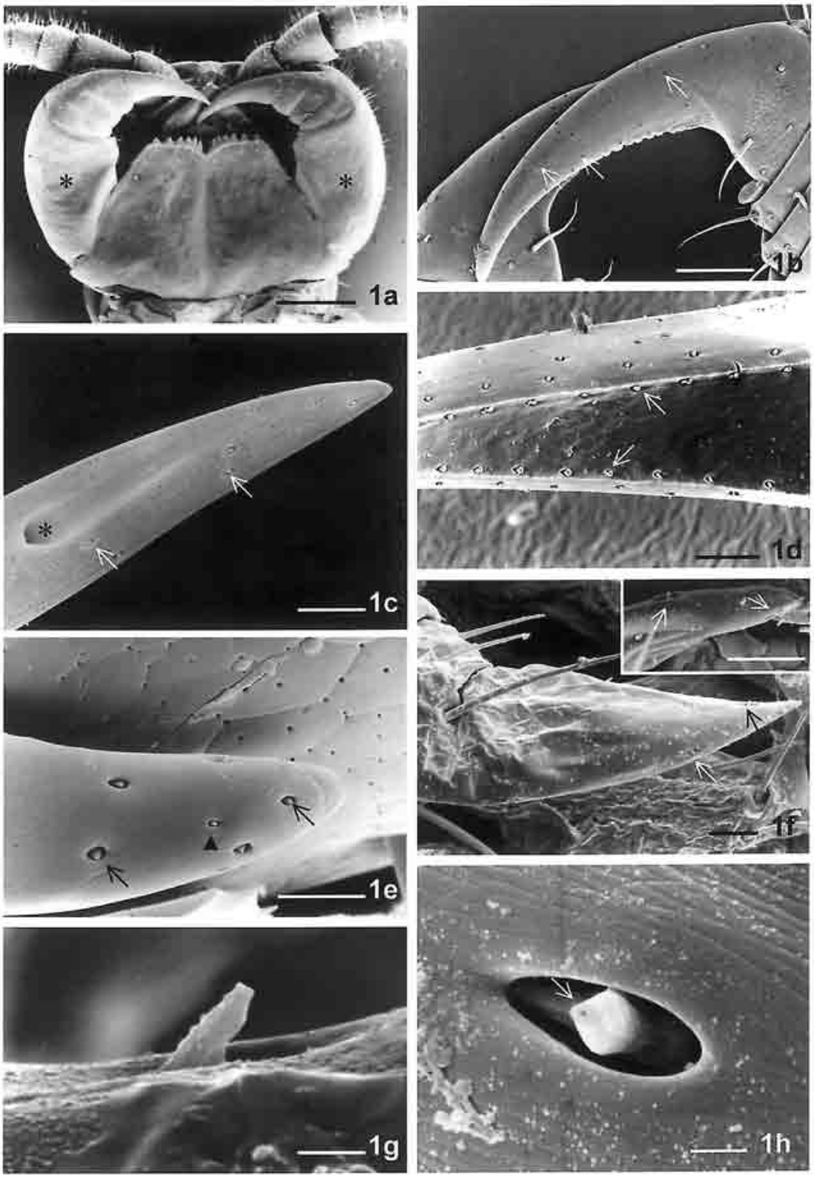


Fig. 1. Distribution of sensilla coeloconica on the poison claws of different centipedes.

a: *Lithobius forficatus*, ventral side of the maxillipedes (*). Scale bar: 0.5 mm. b: *Necrophloeophagus longicornis*, ventral side of the poison claws with many sensilla coeloconica (arrows). Scale bar: 50 µm. c: *Scutigera coleoptrata*, tip of a poison claw with several sensilla coeloconica (arrows) and the opening of the poison gland (*). Scale bar: 10 µm. d: *Asanada socotrana*, part of the inner side of a poison claw with two rows of sensilla coeloconica type III (arrows). Scale bar: 50 µm. e: *N. longicornis*, tip of a poison claw with sensilla coeloconica type I (arrows) and type II (arrowhead). Scale bar: 5 µm. f. *L. dentatus*, larva I, ventral side of a poison claw with sensilla coeloconica (arrows). Scale bar: 10 µm. Inset: *L. mutabilis*, larva I: Sensilla coeloconica (arrows) on the tip of a poison claw. Scale bar: 10 µm. g: *L. dentatus*, larva I, sensillum coeloconicum on the inner side of a poison claw. Scale bar: 1 µm. h: *L. forficatus*, sensillum coeloconicum of type I with a terminal pore (arrow). Scale bar: 1 µm.

1758), *Craterostigmus tasmanianus* (Pocock, 1902), *Asanada socotrana* (Pocock, 1899), *Cryptops hortensis* (Leach, 1815), and *N. longicornis*, preserved in 70 % ethanol, were mounted on Leit-Taps (PLANO) and sputtered with a 25 nm gold film (BALTEC SCD 005). The maxillipedes were examined with a SEM (LEO 1450 VP) and with a Zeiss DSM scanning electron microscope.

For transmission electron microscopic investigations maxillipedes of *N. longicornis* were fixed in 3 % glutaraldehyde (cacodylat-buffer pH 7.4), postfixed in 2 % osmium tetroxide (same buffer) and embedded in DURCUPAN ACM. Maxillipedes of *L. forficatus* were fixed in a modified Karnovsky fixative, containing paraformaldehyde (2 %) and glutaraldehyde (2.5 %) in phosphate-buffered saline (PBS; pH 7.2), and postfixed in 2 % OsO_4/PBS (pH 7.2). Objects were embedded in Epon 812. Ultrathin sections were stained in uranyl acetate and lead citrate and examined with a TEM TESLA BS 500 and a ZEISS 109T.

RESULTS

Morphology and distribution

The maxillipedes of centipedes consist of a plate-like coxosternite and two four-segmented telopodites (Figs 1a, 3). Each telopodite comprises a large prefemur, an annular femur and tibia, and an enlarged tarsus, which forms the medially curved poison claw (Figs 1b, 4). The opening of the poison gland is located close to the tip of the claw, subterminally, on the dorsal side (Fig. 1c). At the base of the poison claw several hair-shaped sensilla trichodea and some peg-shaped sensilla microtrichodea are present. In the anamorphic larval lithobiomorph and in adult centipedes, numerous sensilla coeloconica are distributed over the distal part of the tarsus (Figs 1b, f). Each sensillum coeloconicum consists of a short sensory peg situated in an oval or round pit (Fig. 1e). On the ventral side of the poison claw we counted in *S. coleoptrata* 51, in *L. forficatus* 74, in *C. tasmanianus* 132, in *A. socotrana* 103, and in *N. longicornis* 58 sensilla coeloconica. In all species the density of sensilla increases from the base (2–4/50 μm^2) to the tip of the claw (5–7/50 μm^2) (Table 1).

In the anamorphic larval stages I and II of *L. mutabilis* and *L. dentatus*, only a few sensilla coeloconica are present (>10) on the outermost third of the poison claw (Fig. 1f). All sensilla belong to the same type. Each larval sensillum coeloconicum consists of a slender and acute peg, which is set in a round to oval pit (Fig. 1g). Each sensillum bears a terminal pore. The shaft of the sensillum projects only a little beyond the rim of the pit.

In adults of different groups of centipedes, three types of sensilla coeloconica are distinguishable: Type I: thick, mostly conical sensilla, type II: thin sensilla with rounded tips, and type III: long and tapered sensilla.

The three types are located on different sites of the tarsal segment of the maxillipede. Type I: Numerous type I sensilla coeloconica are distributed on the dorsal and the ventral sides of the poison claw (Fig 1b). Each thick sensillum consists of an acute conical peg, which is set in a circular to oval pit (Figs 1h, 2a, b). The surface of the peg's shaft appears smooth. The socket of the peg is attached by a more or less folded, cuticular membrane to the wall of the pit. At the tip of the peg there is a single terminal pore (up to 0.12 µm in diameter). In *N. longicornis* and *C. hortensis* the terminal pores are often sealed by secretory material and are therefore difficult to detect. The length of

TABLE 1.

Dimensions, numbers, and distribution of sensilla coeloconica on the poison claws of adult centipedes: (n.d.) not determined, (+) present, (?) not clear, (Ø) diameter.

	Scutigera coleoptrata	*Lithobius forficatus*	*Craterostigmus tasmanianus*	*Asanada socotrana*	*Necrophloeophagus longicornis*
Thick sensilla coeloconica (type I)					
Ø peg (µm)	0.97–1.17	1.63–2.39	2.04–3.2	1.96–3.13	1.2–1.61
peg length (µm)	up to 2.33	up to 3.2	up to 4.83	up to 5	up to 2
Ø pit (µm)	2.53–4.4	5.49–9.66	5.38–9.68	3.22–8	2.8–4
terminal pore	(+)	(+)	(+) (Ø 0.12 µm)	(+)	(?)
Thin sensilla coeloconica (type II)					
Ø peg (µm)	0.71–0.87	1.22–1.43	(n.d.)	0.8–1.08	0.8–1.32
peg length (µm)	up to 1.53	up to 2.72	up to 2.6	up to 2.6	up to 1.59
Ø pit (µm)	2.08–3.3	6.21–7.33	4.1–6.88	3.65–6.08	1.05–3.4
terminal pore	(+) partly large pores	(+)	(+) (Ø 0.4 µm)	(+)	(+), mostly small pores
Long sensilla coeloconica (type III)					
Ø peg (µm)	0.81–1.26	1.2–1.49	1.35–1.88	1.45–2.29	0.6–1.2
peg length (µm)	up to 1.95	up to 4.09	up to 4.46	up to 6.38	up to 2.69
Ø pit (µm)	1.63–4.84	8.52–10.3	6.2–9.3	4.76–9.3	2.93–3.5
terminal pore	(+)	(+)	(?)	(?)	(?)
Number of sensilla coeloconica (type I–III)					
dorsal side	35	69	130	(n.d.)	35
ventral side	33	74	132	103	58
inner side	(n.d.)	(n.d.)	40	41	(n.d.)
Density of sensilla coeloconica (type I–III)					
ventral side base	(n.d.)	3/50 µm^2	2–3/50 µm^2	4/50 µm^2	3–4/50 µm^2
ventral side tip	6/50 µm^2	6/50 µm^2	4-5/50 µm^2	7/50 µm^2	6–7/50 µm^2

the pegs varies from 1.95 µm in *N. longicornis* to 5 µm in *A. socotrana*, and the diameters range from 0.97 µm in *S. coleoptrata* to 3.2 µm in *C. tasmanianus*. The diameters of the pit are also different and range from 2.53 µm in *S. coleoptrata* to 9.7 µm in *C. tasmanianus*.

Type II: A few type II sensilla coeloconica (n<10) are concentrated at the tip of the poison claw (Figs 1e, 2c–e). Each thin sensillum consists of a slender peg, which is set in a circular to oval pit (1.05–7.33 µm in diameter). The surface of the shaft of the peg appears smooth. The diameters of the terminal pores are different; in *S. coleoptrata* they are large, whereas they are small in *L. forficatus* (Figs 2c, e). Often the terminal pores of the type II sensilla are sealed by secretory material. In *S. coleoptrata* the length of each peg is about 1.53 µm and in *L. forficatus* it is about 2.72 µm. The diameter of the pegs range from 0.71 µm in *S. coleoptrata* to 1.81 µm in *A. socotrana*. The socket of the peg is attached by a more or less folded cuticular membrane to the inner wall of the pit (Fig. 2c).

Type III: Around 40 type III sensilla coeloconica are concentrated in two rows on the inner side of the poison claw (Fig. 1d). In all the species investigated the peg is centrally

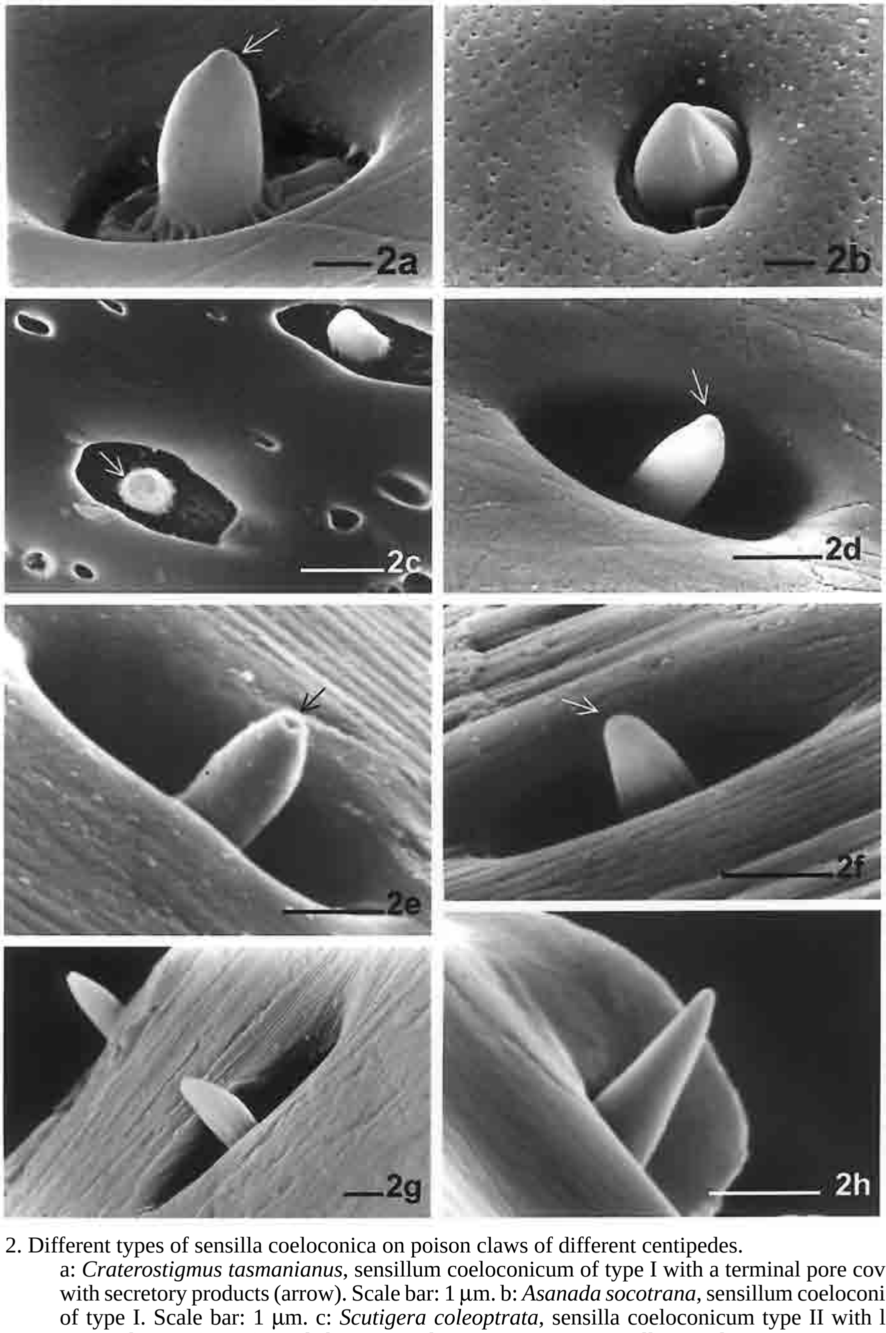
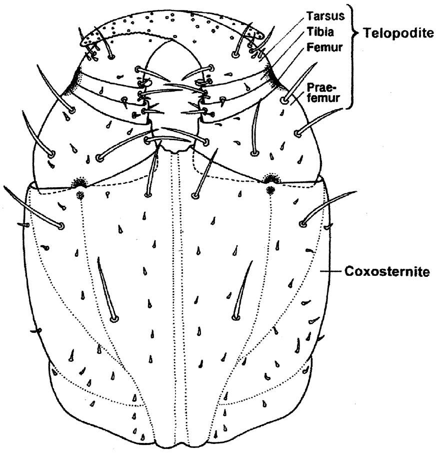


Fig. 2. Different types of sensilla coeloconica on poison claws of different centipedes.
a: *Craterostigmus tasmanianus*, sensillum coeloconicum of type I with a terminal pore covered with secretory products (arrow). Scale bar: 1 µm. b: *Asanada socotrana*, sensillum coeloconicum of type I. Scale bar: 1 µm. c: *Scutigera coleoptrata*, sensilla coeloconicum type II with large terminal pores (arrow). Scale bar: 1 µm. d: *C. tasmanianus*, sensillum coeloconicum type II with a terminal pore covered with secretory products (arrow). Scale bar: 1 µm. e: *Lithobius forficatus*, sensillum coeloconicum type II with a terminal pore (arrow) situated on the tip of a claw. Scale bar: 1 µm. f: *S. coleoptrata*, sensillum coeloconicum type III with a terminal pore (arrow). Scale bar: 1 µm. g: *L. forficatus*, sensilla coeloconica type III. Scale bar: 1 µm. h: *Necrophloeophagus longicornis*, sensillum coeloconicum type III, with a plate-like protrusion. Scale bar: 1 µm.



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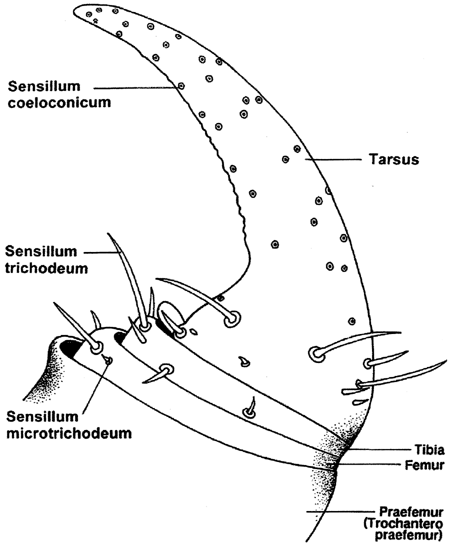

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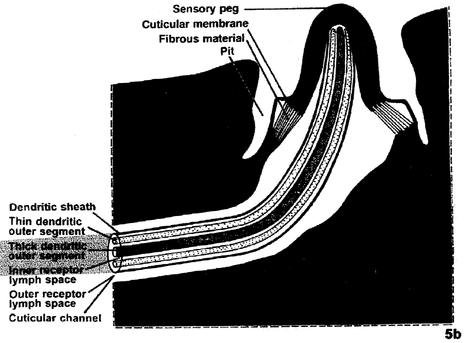

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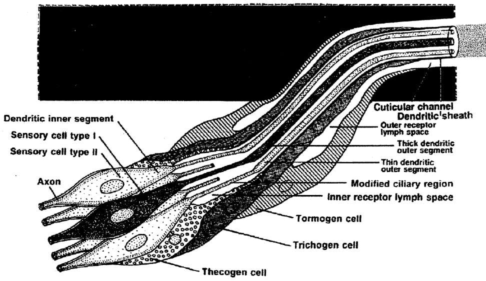

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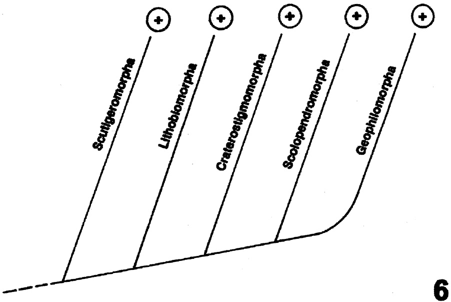

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Figs 3–6. Characters of maxillipedes. 3–4. *Necrophloeophagus longicornis*. 3. Ventral side of maxillipede (schematic). 4. Ventral side of left telopodite (schematic). 5. Diagram of sensillum coeloconicum (type I). a: Complex of sensory and sheath cells, b: Sensory peg. 6. Diagram showing the presence (+) of sensilla coeloconica on the poison claws in the five orders of centipedes.

set in an elongated pit, and the mostly velvet shaft projects over the rim of the pit (Figs 2f–h). The terminal pore is difficult to detect in *C. tasmanianus*, *A. socotrana*, and *N. longicornis*, possible due to secretory material sealing the pore opening. The length of each peg varies and is about 1.95 µm in *S. coleoptrata* and about 6.38 µm in *A. socotrana*. The diameters of the pegs range between 0.6 µm in *N. longicornis* and 2.29 µm in *A. socotrana*. The diameters of the pit range from about 1.63 µm in *S. coleoptrata* (Fig. 2f) to about 10.3 µm in *L. forficatus*. In *A. socotrana* and in *N. longicornis* a plate-like protrusion beside the peg is noticeable (Fig. 2h).

Further details of size, distribution and quantity of the three types of sensilla coeloconica are summarised in Table 1.

Ultrastructure of thick (type I) sensilla coeloconica

(a) ***Necrophloeophagus longicornis***

The conical thick sensillum coeloconicum on the poison claw of the maxillipede in this species consists of a short peg (1.8–2 µm in length) in a small pit (2.8–4 µm in diameter), and a corresponding complex of three to eight uniciliate sensory cells and of three different sheath cells (Figs 5a, b, 10). Both structures are connected by a long cuticular channel (Figs 7, 8). Near the base of the claw the channel is up to 20 µm long, but in sensilla situated more distally, it is up to 90 µm in length.

The short sensory peg extends only a little beyond the edge of the oval to circular pit. A terminal pore at the tip of the peg is difficult to detect due to viscous material in the pore channel, which seals the terminal pore as a plug. The mobility of the peg is restricted by a stable articulating membrane and by radially orientated tight fibrous material to the base of the peg (Figs 5b, 9).

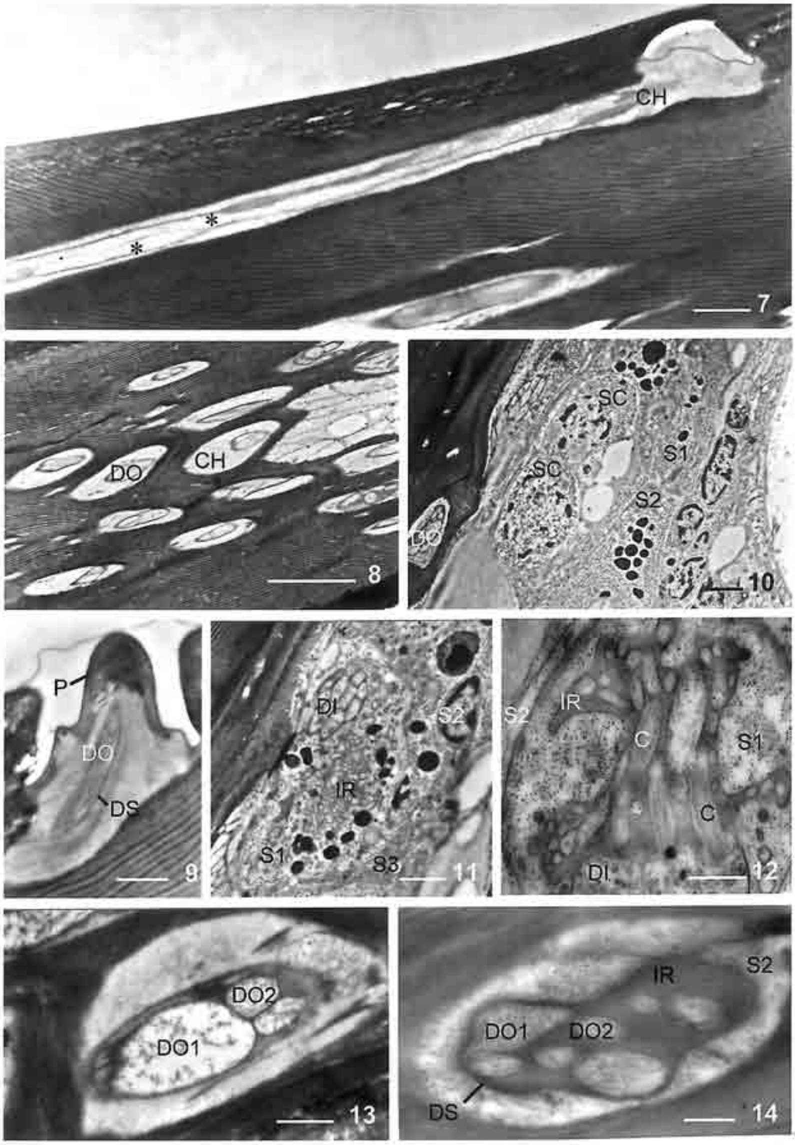
Only a single modified cilium (9 + 0 pattern) arises at the distal pole of each perikaryon of the three to eight sensory cells, i.e. the sensory cell is uniciliate (Fig. 12). One to three thick (0.45–0.75 µm in diameter), and up to 7 thin (0.2–0.35 µm in diameter) dendritic outer segments (Figs 13, 14) are distinguishable. The long dendritic outer segments enter the cuticular channel and terminate in the lumen of the peg (Fig. 9).

The three different sheath cells (thecogen, trichogen and tormogen cell) surround the sensory cells like onion skins and the inner receptor lymph space (Figs 10, 11). The thecogen cell with many electron dense granula terminates at the base of the dendritic sheath, while processes of the trichogen and of the tormogen cell extend into the lumen of the cuticular channel (Fig. 5a). The tormogen cell surrounds a small outer receptor lymph space.

(b) ***Lithobius forficatus***

The conical peg of type I sensilla coeloconica in *L. forficatus* is about 3.2 µm in length, in the region of the socket its diameter is about 2.2 µm. On the level of the peg the diameter of the pit is about 2.4 µm, the length of the pit ranges from 5.5 to 9.7 µm. The base of the peg is connected to the surrounding cuticle by a thin cuticular part (Figs 15, 16). The cuticular channel (diameter about 0.5 µm) of the peg opens at its end in a small terminal pore about 0.2 µm in diameter (Fig. 15). Sometimes viscous material is observed in the pore channel which seals the termial pore as a plug.

Each sensillum is innervated by 7 to 9 distal dendritic outer segments of the sensory cells (Fig. 20). The perikarya house the nucleus and, in addition to other organelles, a



Figs 7–14. *Necrophloeophagus longicornis*. Ultrastructure of thick sensilla coeloconica type I. 7. Part of the cuticular channel (CH) with long dendritic outer segments (*). Scale bar: 2 µm. 8. Transverse sections of several cuticular channels (CH) with dendritic outer segments (DO). Scale bar: 5 µm. 9. Longitudinal section of a sensory peg (P) with dendritic outer segments (DO), surrounded by a dendritic sheath (DS). Scale bar: 0.5 µm. 10. Complex of two sensory cells (SC) and two sheath cells (S1, S2) and dendritic outer segments (DO). Scale bar: 1 µm. 11. Dendritic inner segments (DI) near inner receptor lymph space (IR). S1–S3 thecogen, trichogen and tormogen cells. Scale bar: 1 µm. 12. Transition of the dendritic inner segments into the ciliary region (C) of the dendrites. DI = dendritic inner segment, S1, S2 = thecogen and trichogen cells, IR = inner receptor lymph space. Scale bar: 0.5 µm. 13. Thick (DO1) and thin (DO2) dendritic outer segments in a cuticular channel. Scale bar: 0.5 µm. 14. Thick (DO1) and thin (DO2) dendritic outer segments within inner receptor lymph space (IR). DS = dendritic sheath, S2 = process of trichogen cell. Scale bar: 1 µm.

considerable number of mitochondria. From each dendritic inner segment of the sensory cells only a single modified cilium arises (9 + 0 pattern), i.e. the sensory cell is uniciliate (Fig. 21). The dendritic outer segments enter the long cuticular channel (Fig. 17) and end without branching, just below the terminal pore of the peg. The diameters of the outer segments vary; 2 to 5 thick (diameter 0.6–1.2 µm) and 4 to 7 small (diameter 0.2–0.4 µm) dendritic outer segments are visible (Fig. 20). These outer segments contain microtubules.

Three different sheath cells (thecogen, trichogen, and tormogen cell) surround the sensory cells concentrically (Figs 22, 23). The thecogen cell produces a cuticular dendritic sheath, which encloses the receptor lymph cavity with the dendritic outer segments. The dendritic sheath ends just below the terminal pore and the thecogen cell below the beginning of the cuticular channel. The trichogen cell surrounds the dendritic sheath; projections of this cell are detectable up to the socket of the peg. The tormogen cell ends far from the entrance of the dendrites into the cuticle of the poison claw.

Ultrastructure of type II sensilla coeloconica

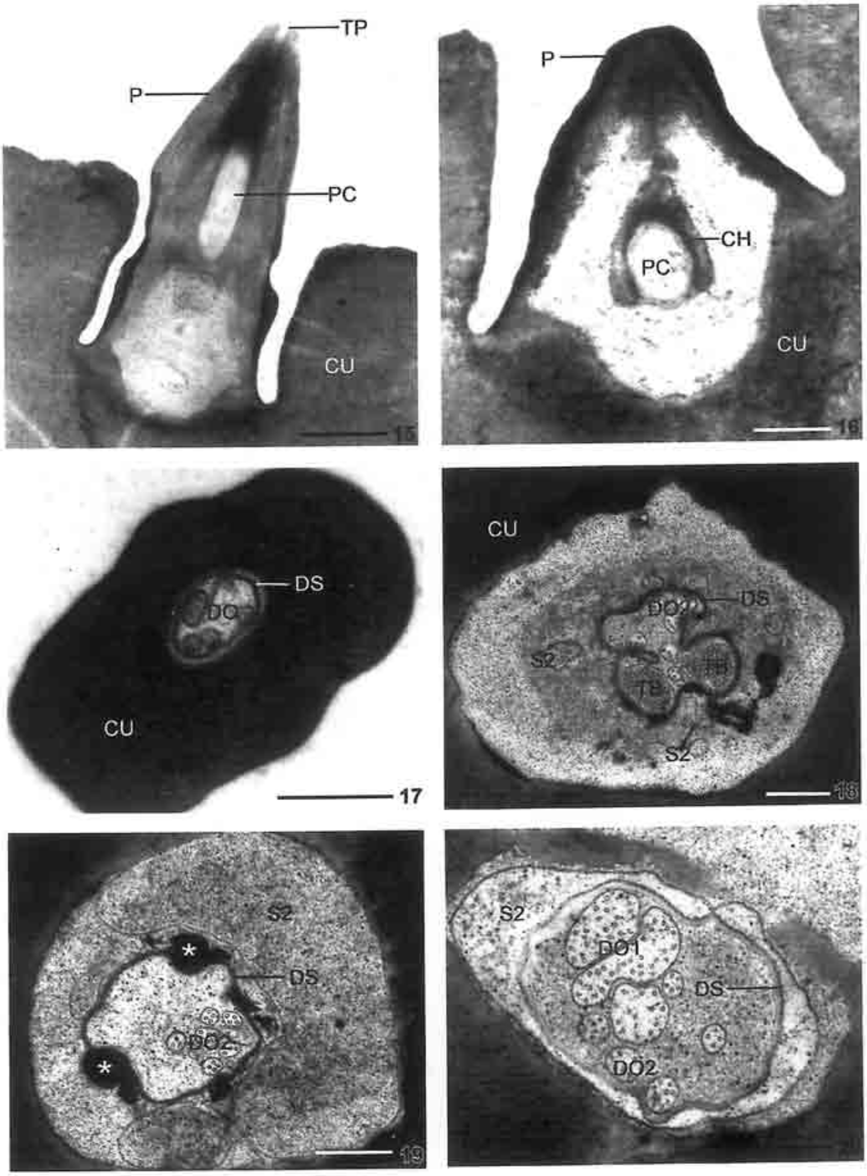
The type II sensilla coeloconica of *L. forficatus* are similar in structure to the type I sensilla (Fig. 23 inset). They differ in that two of the large dendritic outer segments of one sensory cell possess tubular bodies (Fig. 18). The outer segments end with their tubular bodies near to a specific cuticular differentiation, which surrounds the cuticular sheath like a cap on the level with the socket of the sensory peg (Figs 16, 19). The acute tip of the cuticular cap is fused to the cuticle of the shaft of the peg (Fig. 16). The remaining dendrites run up to the terminal pore opening of the sensillum.

There are no ultrastructural data of type III sensillum coeloconicum available.

DISCUSSION

The present investigation has demonstrated the presence of sensilla coeloconica on the poison claws of adult centipedes and anamorphic larvae of the Lithobiomorpha. In adult centipedes three types of these sensilla are distinguishable, which differ in shape, size and distribution: many thick sensilla (type I) distributed on both sides of the claw, few thin sensilla (type II) only located at the tip of the claw, and long sensilla (type III) situated in two rows along the rims of a groove on the inner side of the claw (Ernst & Rosenberg 2001; Rosenberg & Ernst 2001; Ernst *et al.* 2002). The presence of three types of sensilla coeloconica on the poison claw in the adults of all investigated species of the five orders of centipedes (Scutigeromorpha, Lithobiomorpha, Craterostigmomorpha, Scolopendromorpha, and Geophilomorpha) suggests a synapomorphic feature, which demonstrates the monophyly of the centipedes (Fig. 6) (Borucki 1996; Edgecombe & Giribet 2002), but further structural investigations are necessary to confirm this.

Each sensillum coeloconicum is composed of a short sensory peg set in a cuticular pit. The peg projects only a little over the rim of the pit. Each sensillum bears a single pore. Sometimes pore openings are not noticeable in REM-studies, for example in the thick sensilla of *N. longicornis* and *C. hortensis* (Ernst & Rosenberg 2001) or in sensilla of *S. morsitans*, as described earlier by Jangi & Dass (1977). In these cases it is assumed the pores are filled with a plug of viscous material which extends onto the outer cuticle surface. The present SEM and particularly the TEM investigations clearly demonstrate



Figs 15–20. *Lithobius forficatus*, utrastructure of sensilla coeloconica type I and II. 15. Longitudinal section of a type I sensillum coeloconicum with a terminal pore (TP). CU = cuticle, P = sensory peg, PC = pore channel. Scale bar: 1 µm. 16. Oblique section of the base of type II sensillum coeloconicum with cuticular cap (CH), surrounding pore channel (PC). CU = cuticle. P = sensory peg. Scale bar: 1 µm. 17. Transverse section of tip of a sensillum with dendritic outer segments (DO). CU = cuticle, DS = dendritic sheath. Scale bar: 0.5 µm. 18. Transverse section of type II sensillum with small (DO2) and two thick dendritic outer segments with tubular bodies (TB). DS = dendritic sheath, S2 = projections of the trichogen cell. Scale bar: 0.5 µm. 19. Transverse section of type II sensillum with small dendritic outer segments (DO2). Asterisks mark the proximal projections of the cuticular cap. DS = dendritic sheath, S2 = trichogen cell. Scale bar: 0.5 µm. 20. Transverse section of type I sensillum with thick (DO1) and small (DO2) dendritic outer segments filled with microtubules. DS = dendritic sheath, S2 = trichogen cell. Scale bar: 0.5 µm.

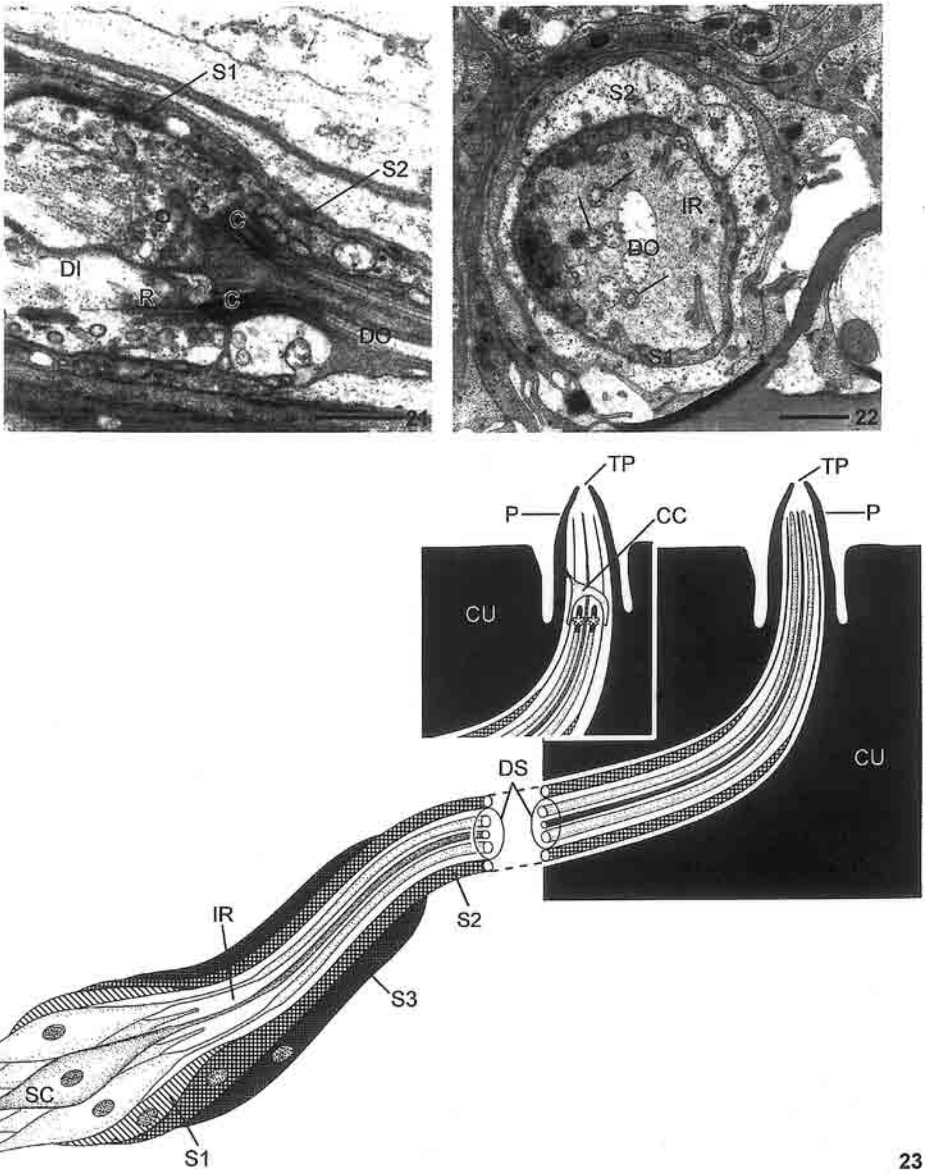
the existence of a single terminal pore in the sensilla coeloconica on the poison claw of centipedes.

In *N. longicornis* the movement of the cuticular peg is reduced, due to specialisation of the cuticle of the socket. In *L. forficatus* the type I and II sensilla exhibit no socket structure; the cuticle in this region is narrow and the sensillum seems to be movable to a certain degree. A special feature of the coeloconic sensilla on the poison claws of the maxillipedes in *N. longicornis* and in *L. forficatus* is a conspicuous, long cuticular channel of 20–90 µm. It connects the perikarya of the sensory cells and sheath cells with the cuticular peg on the surface of the poison claw (Ernst 1995; Ernst & Rosenberg 2001). The extended dendritic outer segments enter the cuticular channel and terminate in the lumen of the peg. As far as we know, such an extensive cuticular channel is only observed in centipedes. The fine structural organisation of the type III sensilla is not known yet, but it is thought that the type III sensilla are of a similar structure to the type I sensilla.

The classification of the sensilla coeloconica on the poison claws of *N. longicornis* and *L. forficatus* based on external and internal morphological features is rather difficult. In other Myriapoda comparable coeloconic sensilla are only known from the antennae of the millipede *Polyxenus lagurus* Linnaeus, 1758 **(**Nguyen Duy-Jacquemin 1983 1997). These sensilla lack a terminal pore and were referred to as no pore-sensilla by Altner *et al*. (1983). The fine structure is different to those of the centipedes: the number of sensory cells is always five, and the sensory cells are both uniciliate and biciliate. One of the sensory cells possesses a lamellated dendritic outer segment. Five sheath cells are present, whereas a dendritic sheath is absent. Based on the fine structure it is assumed that the sensilla of *P. lagurus* function as thermo- and hygroreceptors. Lamellated outer segments are also described by Tichy (1987) at the base of the antennal flagellum in the pauropod *Eurypauropus ornatus* Latzel, 1883.

The fine structural organisation of the hitherto investigated type I/II sensilla coeloconica in *N. longicornis* and *L. forficatus* is rather constant. Each of the sensilla is composed of uniciliate sensory cells and thick and thin unbranched dendritic outer segments are present. The dendrites are always surrounded by 3 sheath cells and a dendritic sheath. Only in the type II sensillum of *L. forficatus* are tubular bodies present; the same is assumed for the type II sensilla of *N. longicornis*, hitherto not investigated. Similar tubular bodies are observable in mechanoreceptive cuticular sensilla of centipedes (Ernst 1976 1983; Keil 1975 1976).

In several insects (*Forficula auricularia* Linnaeus, *Gomphocerippus rufus* L., *Pyrrhocoris apterus* L., *Drosophila melanogaster* Meigen) there are antennal coeloconica-like sensilla, but a terminal pore is absent. These sensilla consist of two or three types of sensory cells with different dendritic outer segments. The long dendritic outer segments of type-1 sensory cells continue into the peg, where they fit tightly to its wall. Type-1 sensory cells are regarded as hygroreceptors (Altner *et al*. 1983). A special feature of the dendritic outer segment of the type-1 sensory cells are numerous parallel microtubules, which resemble the tubular bodies of mechanoreceptive sensory cells of insects (Thurm 1964 1965) and centipedes (Ernst 1976 1983; Keil 1976). In *F. auricularia*, the type-2 sensory cell has a lamellated dendritic outer segment, which terminates beneath the peg. The type-2 sensory cell is thought to be a thermoreceptor. The type-3 sensory cell, only present in *F. auricularia*, has a short dendritic outer segment with unknown function (Altner *et al*. 1983).



Figs 21–23. *Lithobius forficatus*, ultrastructure of sensilla coeloconica, type I and II. 21. Longitudinal section of ciliary region (C) with dendritic inner (DI) and outer segments (DO). R = striated rootlets, S1 = thecogen cell, S2 = trichogen cell. Scale bar: 1 µm. 22. Transverse section of ciliary region (lines) and dendritic outer segments (DO). IR = inner receptor lymph space, S1 = thecogen cell, S2 = trichogen cell. Scale bar: 1 µm. 23. Diagram of basal (left) and distal part (right) of type I sensillum coeloconicum. Inset: distal part of type II sensillum coeloconicum with tubular bodies (*). CC = cuticular cap, CU = cuticle, DS = dendritic sheath, IR = inner receptor lymph cavity, P = sensory peg, SC = sensory cell, S1 = thecogen cell, S2 = trichogen cell, S3 = tormogen cell, TP = terminal pore.

Yokohari (1978 1981) found lamellated dendritic outer segments in the antennal hygro- and thermoreceptive sensillum capitulum, a no-pore sensillum (np-sensillum) of the cockroach *Periplaneta americana* Linnaeus. A further np-sensillum is the antennal coelocapitular sensillum of the honeybee *Apis mellifica* Linnaeus (Yokohari 1983). Only the latter sensillum clearly resembles the sensillum coeloconicum on the maxillipedes of centipedes. The coelocapitular sensillum likewise functions as a hygro- and thermoreceptive sensillum, but there is no lamellated dendritic outer segment.

The function of sensilla coeloconica on the maxillipedes of centipedes remains unclear, as electrophysiological data are lacking. The existence of terminal pores on the tips of the pegs in coeloconic sensilla of larval and adult centipedes points to a possible chemoreceptive function which is shown by Jangi & Dass (1977) in *S. morsitans* by behavioural experiments. On decapitated heads the receptors of maxillipedes were stimulated by glucose solution. This evokes an instantaneous feeding reflex by movement of the mouth parts. Additionally, the presence of tubular bodies in two dendritic outer segments of type II sensilla coeloconica in *L. forficatus* suggests a combination of mechanoreceptive and chemoreceptive sensory cells. These sensilla may serve as contact chemoreceptors or gustatory sensilla (Rosenberg & Ernst 2001).

The existence of thick and thin types of dendritic outer segments within the type I sensilla coeloconica in the Geophilomorpha and Lithobiomorpha points to a dual function of these sensillae, perhaps to thermo- and hygroreception, but pure chemoreception cannot be excluded (Ernst 1995 2000; Ernst & Rosenberg 2001). Such a dual function was also presumed in the antennal coeloconic sensillae of the millipede *P. lagurus* (Nguyen Duy-Jacquemin 1983). It is assumed that the sensilla coeloconica on the poison claws of adult centipedes are involved in the detection of prey, in the analysis of its components, and in the control of the penetration of the poison claws into the prey.

The presence of coeloconic sensillae with terminal pores in anamorphic larvae of Lithobiomorpha is surprising. During the anamorphic larval stadia I/II these animals do not take up food; they feed on their yolk reservoir within the gut (Scheffel 1969). Their maxillipedes are not necessary for catching prey, and the sensilla are not needed for testing the composition of prey. So a chemoreceptive or gustatory function is not expected. It is assumed the organisation of the larval sensilla coeloconica is similar to that of the adult, so the functions are probably hygro- or thermoreception.

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